THE EYES OF *ASAPHUS RANICEPS* DALMAN (TRILOBITA)

by E. N. K. CLARKSON

ABSTRACT. The holochroal eyes of the Lower Ordovician trilobite *Asaphus raniceps* Dalman have been studied using light and electron microscopy.

In these eyes the refractive elements are elongated calcite prisms underlying a cornea which is continuous with, although structurally dissimilar to, the 'outer cuticular layer' described by Dalingwater. The prisms are orientated with their *c*-axes normal to the surface. Some of the material studied (from Öland) showed the effects of at least two phases of diagenesis, which in one case had resulted in the production of secondary prisms growing syntaxially on the primary prisms, and confusingly similar to primary structures.

The visual surface approximates a segment of an almost perfect spheroid whose radii of curvature in vertical and horizontal planes all converge to a single point, in a manner very similar to that of some superposition eyes in modern arthropods, with which analogies are drawn.

Problems in the use of calcite as a primary refractive medium are discussed, and it is concluded that the effects of birefringence could have been minimized by suitable pigment screens, like those of insects and crustaceans, underlying the prismatic layer.

The 'sensory fossettes' on the eye-socle are craters, each with a central perforation communicating with the internal surface.

TRILOBITES of the family Asaphidae have distinctive compound eyes whose range in form is quite well known from palaeontological literature. These eyes, often well preserved, are usually rather large and prominent, and often rise above the glabella; one remarkable species, *Asaphus kovalevskii* Lavrov, has eyes situated upon very elongated bases resembling long stalks. Asaphid eyes were referred to by various authors working in the nineteenth and early twentieth centuries; Schmidt's (1904) monograph, for instance, contains good illustrations. More recent authors have also described and figured asaphids with intact eyes, and Whittington's studies (1963, 1965) included many details of external eye morphology. Hupé (1953) has provided an excellent figure of the eye of *Asaphus cornutus* (Pander), reproduced in the 'Treatise' by Harrington (1959), and Rose (1967) has shown that in *Nileus* and *Isotelus* growth of the visual surface is accomplished by the addition of new lenses round the lower margin of the eye.

Although we possess a reasonably good understanding of the range in form and external morphology of asaphid eyes, there have been only two serious attempts to investigate their internal morphology; the first being that of Lindström (1901), who described sections and fracture surfaces of the eyes of several Scandinavian asaphids. He showed that the refractive elements were elongated prisms (rather than lenses) underlying the cornea, and gave a good account of their anatomy. Balashova (1948) confirmed that the eye had a prismatic structure, and further indicated that the eye-socle (Lindström's reticulate or spongious zone) was permeated with very fine pore-canals and that there were 'fossae' on the socle opening downwards into fine calcite-filled tubes, to which she imputed a sensory (tactile) function. The advent of the scanning electron microscope stimulated further study of the eyes of asaphids, and, as expected, revealed many details invisible to Lindström.

In 1967 Dr. John Dalingwater kindly sent me a number of finely preserved specimens of *Asaphus* which he had collected from Böhlin's (1949) locality where the glauconitic '*raniceps*' limestone is exposed at the cliff of Haget, northern Öland. Tjernvik (1972, p. 305) gives the age of this limestone as lower Llanvirnian (*bifidus* zone). Specific identification of these was somewhat difficult as most of the specimens were fragmentary, but Dr. Dalingwater and I agree that they most closely approximate *A. raniceps* Dalman, *sensu* Angelin (1878, p. 53).

During the investigation of these eyes, using light and electron microscopy, it became evident that different specimens had been variously affected by diagenesis. This made the interpretation of the original structure difficult, for it was not immediately apparent in all cases which structures were primary and which were the results of secondary recrystallization. In one specimen, for instance, there were radially arranged microstructures extending quite deep inside the eye, these were so regularly formed that they could have been mistaken for primary structures, but they proved, in fact, to be secondary, growing syntaxially upon primary elements of the 'refractive' zone.

Part of this study has been therefore orientated towards an understanding of the nature of primary structures and how they were affected by diagenesis; the rest is more closely concerned with the organization of the eye as a functional visual organ.

The specimens were prepared for examination as follows. The prefix 'Gr I' refers to the collections of the Grant Institute of Geology, University of Edinburgh.

External surface only. Gr I 5501.

Internal structure using thin sections, polished surfaces, and cellulose peels. Gr I 5502, 5503, 5510, 5511, 5512.

External and internal features (fracture surfaces and etched sections) using the Stereoscan. Gr I 5504, 5505, 5506, 5507, 5508, 5513.

THE CUTICLE OF *ASAPHUS*

Dalingwater (in press) in a study of the structure of trilobite cuticles has shown that *Asaphus raniceps* (from the same locality as my material) has a cuticle of two distinct layers. The outer layer, less than one-tenth of the total thickness, is composed of fairly regular perpendicular crystallites which have a fibrous appearance. The thick inner area is less distinctly structured, and no individual crystallites could be seen. Neither layer extinguished uniformly in polarized light implying that the calcite of which the bulk of the cuticle is composed does not occur in regularly arranged crystallites. There was also some organic matter remaining, which could be isolated by decalcifying the cuticle with EDTA.

These two cuticular layers have their direct counterparts in the eye. The thin outer layer passes laterally into the cornea, losing its fibrous appearance at the periphery of the eye-socle, and becoming thinner. The thick inner cuticular area is directly equivalent to that part of the eye underlying the cornea, consisting of large hexagonal prisms of calcite, which acted as refractive units, directing light to the photoreceptive organs below. These large prisms unlike the inner cuticular area are regularly structured and have their *c*-axes orientated near normal to the outer surface of the eye.

VISIBLE STRUCTURES IN THE EYE OF *ASAPHUS RANICEPS*

External surface. The external form of the eye (text-fig. 1a–c) closely approximates that of *Asaphus cornutus* Pander, from the Ordovician of Estonia, figured by Hupé (1953, p. 77, fig. 31) and reproduced by Harrington (1959, p. O.88, fig. 64i). It is large and strongly curved in plan, projecting well above the glabella. The visual surface, which has a much higher profile curvature anteriorly, is situated upon a vertical 'eye-socle' rising abruptly from the librigena (*sensu* Shaw and Ormiston 1964), upon which are shallow funnel- or basin-shaped cavities, irregularly distributed and decreasing in size towards the base of the eye-socle. These were described by Hupé as sensory fossettes. The facial suture is semicircular, separating the visual surface from the palpebral lobe, which slopes sharply down to the glabella, and carries terrace-line ornamentation.

There is a thin pellucid cornea covering the surface, merging laterally into the outermost layer of the cuticle (text-fig. 4c; Pl. 50, fig. 9). Through this cornea the many quadrate or hexagonal lenses can be seen by translucence, especially if the specimen is immersed in a medium of high refractive index. Hupé's specimen showed patches of larger irregularly distributed lenses, which he thought had resulted from damage during ecdysis.

Even with the Stereoscan the external surface of the best-preserved specimens appears to be smooth and structureless; a microgranular effect is not evident until magnifications of over ×500 is reached. Relative granularity, however, varies according to the quality of preservation of the material.

Internal structure. Lindström (1901, pp. 28, 37–43, pl. 1, figs. 8–30) gave a good account of the eye structure in asaphids as known to him, and noted the following main points. Welded to the inner surface of the cornea are the refractive organs, appropriately termed prisms, which are closely packed hexagonal pillars, arranged radially. (This zone is here termed the primary prismatic region.) If the eye is fractured the prisms separate cleanly from one another, and can be seen under low magnification like columns of basalt lying on their sides. Vertical sections show that the prisms generally become longer and thinner near the margins of the eye, and especially towards the lower rim of the visual surface.

Above and below the visual surface the prisms pass into a rather structureless 'marginal zone', twice as thick (in section) as the primary prismatic region. Lindström referred to this also as the 'spongious' or 'reticulate' zone, in view of its spongy appearance in slightly decomposed specimens. He noted the fossettes on the eye-socle also but did not impute a sensory function to them.

The use of the Stereoscan has given more information upon the nature of most of these regions, and most particularly of the primary prismatic layer.

In the best-preserved specimens, each prism is a single crystal of calcite with its optic axis normal to the surface (text-fig. 1d). The optic axes of neighbouring prisms diverge slightly. Thin sections made horizontally through a complete eye and examined using crossed nicols show that the prisms undergo extinction in the NS. and EW. positions; this pattern remains constant on rotation. Tests with a sensitive tint plate show that the *c*-axes of the calcite crystals are normal to the surface. It is difficult to imagine how such a system as this, with regularly diverging optic axes,

can be other than primary, for although further impregnation with calcite during diagenesis might take place in optical continuity with the existing crystal lattices, more extensive recrystallization would very likely destroy the regularity of the pattern, as has actually happened to some extent in some of the less well-preserved specimens. The eyes in living specimens of *Asaphus raniceps* must therefore have had a high
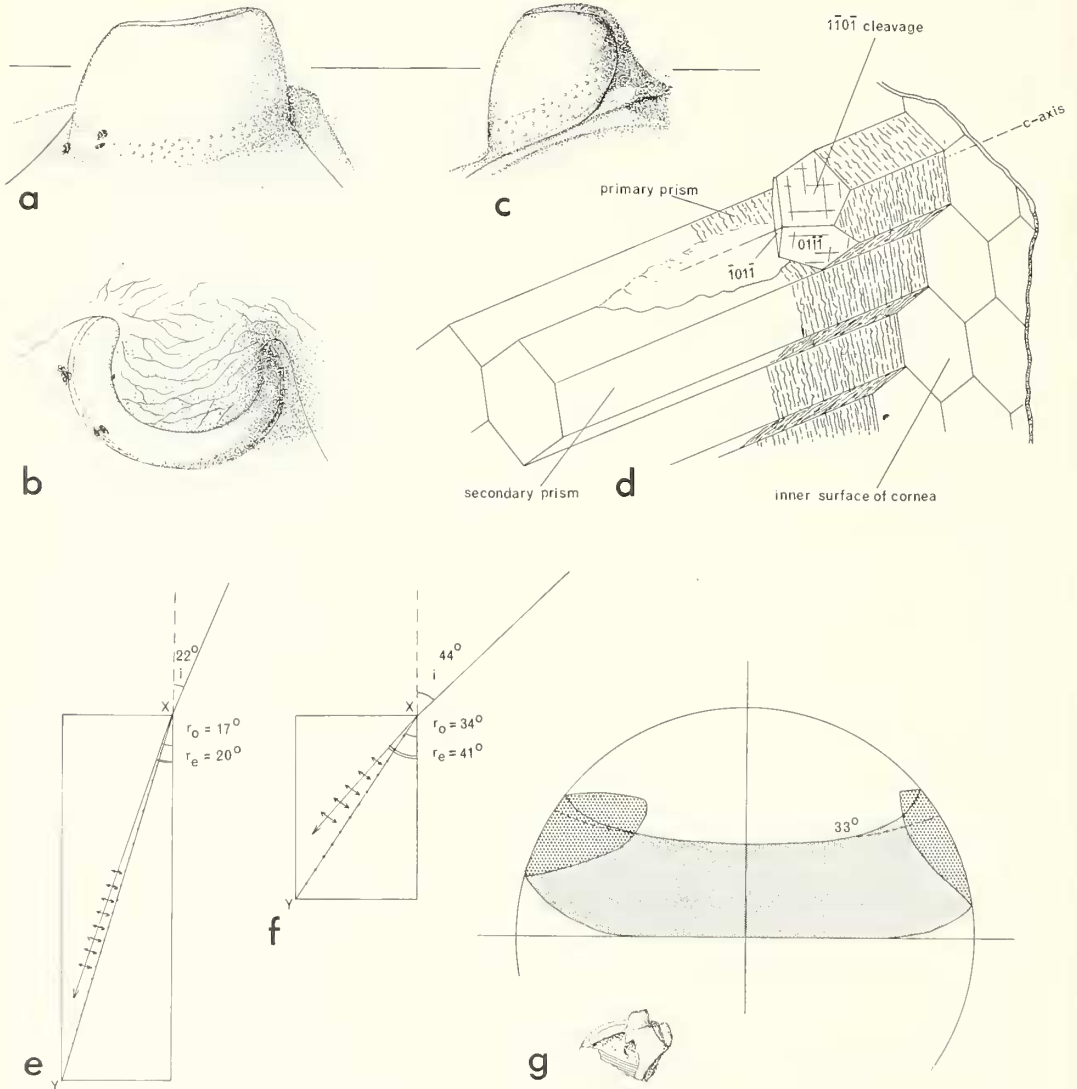
TEXT-FIG. 1. *a–c*. Left eye of *A. raniceps* Dalman. ×6·5. Gr I 5501, in lateral, dorsal, and posterior views. The black specks are adherent glauconite grains. *d.* Diagrammatic construction showing crystallography of the primary and secondary (diagenetic) prisms underlying the cornea. *e–f.* Polarization of light rays passing through a peripheral (*e*) and a central (*f*) primary prism. The o-ray (*XX*) is shown passing along the long diagonal (*XY*). For full explanation see text, p. 438. *g.* Minimal visual field of *A. raniceps*, from Gr I 5501, orientated as in the small diagram (the latter ×2/3).

proportion of calcite, each prism being a single calcite crystal, presumably associated with protein and other organic material.

It is not surprising to find calcite used as a structural component in the eyes of trilobites, for many modern arthropods which have cuticles reinforced with calcite are found to have calcite in the eye as well. It is not, however, used in the same way, for although the prisms of *A. raniceps* have an extremely regular arrangement, there is no regularity of structure in the rest of the cuticular inner area. The arrangement of calcite crystals in the eyes and cuticle of many modern arthropods is singularly irregular. According to Richards (1951, pp. 103–105), crystallization of calcite in very many modern arthropods begins independently at various loci and each crystal simply continues growth until it contacts another crystal. This is true for the calcite crystals within the eye as well, as Düdich (1931) clearly showed; for randomly orientated calcite crystals cut across the ommatidia at all angles without any relationship at all to organic boundaries. In *A. raniceps* on the other hand each visual unit, or at least the upper part, was individually calcified, and, as argued later, calcite was probably the primary refractile material.

In thin sections the cleavages in the prisms often appear distinct, each prism having its own set of cleavages, orientated slightly differently to its neighbours. Not infrequently, however, two or three neighbouring lenses in some sections can be seen to have the same cleavages running through all of them, and the small block or 'domain' of lenses goes into extinction as a unit with sharply marked edges. Rotation of the stage thus produces a stepwise rather than a regular extinction. It is likely that such domains were secreted together and retained their optical continuity throughout life. It has been suggested to me by C. Eccles that this may have resulted from a crystallographic constraint, and that neighbouring prisms had to grow in the same optical orientation as the angle of divergence of individual prisms was too small to permit crystallographic separation. Only when there was a critical angle of divergence could another domain grow at a different crystallographic orientation. It is not clear whether new prisms were always secreted in domains but it is not unlikely, for the individual prisms often seen in section with separate orientation could belong to a small domain of three or four lenses of which only one was cut in the plane of the section.

The tendency for small groups of neighbouring lenses to have the same crystallographic orientation is shown also in Stereoscan photographs, such as Pl. 49, fig. 3 where two adjacent prisms lying below the cornea have cleavages running through both of them without a break.

The sides of intact prisms as shown in Stereoscan photographs are remarkably rough, with corrugated granular surfaces (Pl. 48, figs. 1–3; Pl. 49, fig. 5). These corrugations are always parallel with the cornea, and are related to the underlying cleavage directions (text-fig. 1*d*). Usually, though not always, the prisms become long and thin towards the top and particularly the bottom of the visual surface (Pl. 48, fig. 2). Here they may be up to twice the length in other parts of the eyes. In some specimens, however, this tendency is far less evident. It is possible that the former condition occurs only in immature specimens. It is clear that the new visual units must, as in Phacopina (Beckmann 1951; Clarkson 1966*a*) have been produced in a generative zone at the periphery of the eye and the work of Rose (1967) confirms

that they were added only at the base of the visual surface. In *Asaphus* the genera-
tive zone seems to have lain at the lower junction of the visual surface and the marginal
zone. New prisms were first of all the same width (in section) as the marginal zone
and very thin; they shortened and grew thicker as they became functional.

Some of Lindström's specimens showed concentric layering within the lenses.
Such concentric structure was not visible in any of my material, and neither did
etching with dilute acid (Pl. 48, fig. 5) reveal any structures other than the cleavages
which were picked out by the acid. The apparent absence of layering may have been
because Lindström's material was less fresh than mine, and that mild weathering
might have revealed primary structures in his specimens which were not clear or
evident in mine though they may have been present.

The sensorial fossettes. Hupé (1953) noted a series of irregularly distributed, shallow
excavations on the eye-socle, which he described as sensorial fossettes. Lindström
(1901) had previously noted the presence of these little pits, but imagined them to
be the excavations of some boring organism. Some thin sections and polished sur-
faces made in the present study showed that each fossette is set at the summit of a
narrow canal (now calcite filled) which can be traced to the inner surface of the eye-
socle though little structure can be seen, even in the posterior part of the socle where
the best and largest examples are normally located (text-figs. 4*a*, *b*, *c*; Pl. 50, fig. 9).
Stereoscan photographs of the external surface simply show the fossettes as shallow
rimless craters and contribute nothing further to our knowledge (Pl. 48, fig. 6).

Hupé's interpretation of the fossettes as sensory structures seems appropriate;
similar structures in the neighbourhood of some insect eyes are the sites of vibro-
sensory organs whose nerves are connected with the third optic lobe (Burtt and
Catton 1966*a*). Very many trilobite eye lobes are provided with pit-like structures,
narrow vertical grooves, small tubercles (often only properly visible with the Stereo-
scan), or other such organs, usually located on the eye-socle; these may all be the
sites of sensory organs of some kind, hence the fossettes of *Asaphus*, though excep-
tionally large, are not unusual amongst the trilobites.

EFFECTS OF DIAGENESIS

Recrystallization of the primary prisms. The course of diagenesis was followed in
thin sections of the eyes of different specimens following Friedman (1964). Some
sections, or parts of sections, showed the original form of the calcite prisms, either
as single crystals or as small domains. In these, the cleavages are always distinct

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EXPLANATION OF PLATE 48

Asaphus raniceps Dalman (Stereoscan photographs all of fracture surfaces except figs. 5 and 6).

Fig. 1. Prisms near lower margin of the visual surface. ×110. Gr I 5505.
Fig. 2. Elongated prisms near the lower margin of the visual surface. ×440. Gr I 5504.
Fig. 3. Corrugated surfaces of prisms in the central part of the eye. ×2300. Gr I 5507.
Fig. 4. Similar prisms showing cleavages parallel with the corrugations. ×1100. Gr I 5507.
Fig. 5. Horizontal ground surface, cutting through prisms and etched with dilute HCl. ×525. Gr I 5510.
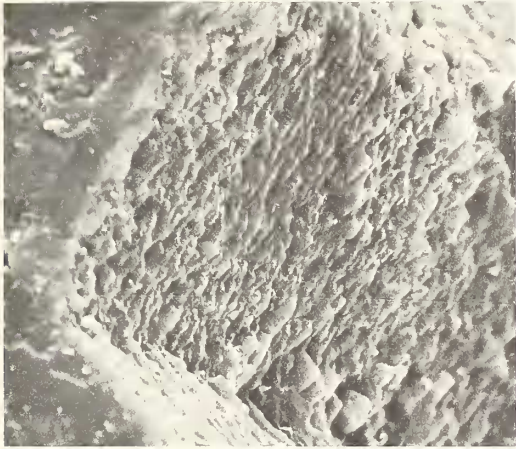Fig. 6. Surface of the eye-socle in the posterior region, showing sensory fossettes. ×110. Gr I 5507.
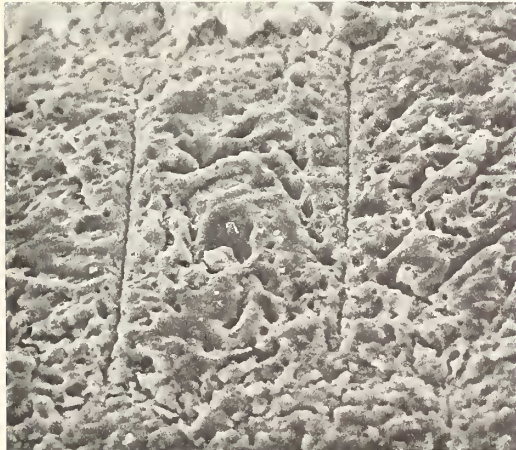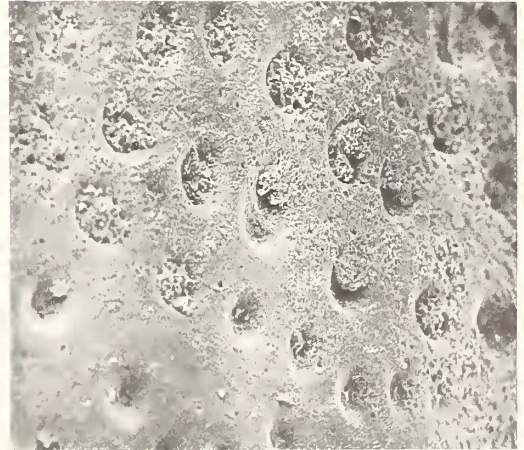
PLATE 48

CLARKSON, *Asaphus* eyes

(Pl. 50, fig. 1), and extinction follows a stepwise pattern. The lower ends of the prisms may be rounded or somewhat ragged in appearance, but never show crystal faces.

Two stages of diagenesis have been differentiated. The first stage involved some degree of recrystallization of calcite *in situ*, into a microcrystalline form, resulting in the crystal boundaries and cleavages becoming indistinct, and blurring the extinction pattern (Pl. 50, fig. 6). This was seen in its early stages in certain parts of otherwise unaltered eyes. The recrystallized areas (yellow-brown under crossed nicols) are often darker in colour than the primary crystals.

In some sections diagenesis has been carried a stage further, with a second development of microcrystalline calcite invading the already altered primary prismatic region (Pl. 50, figs. 7, 8). This second stage microcrystalline calcite is variable in colour, but is usually a very light yellow, contrasting with the darker yellow-brown of the first-stage diagenetic material. Sometimes it appears as randomly orientated flecks or patches within the prisms. Often it is seen as a 'front' which has advanced into the prismatic region from either surface. On occasion it has picked out the boundaries of the altered prisms, which then appear as thin yellow lines, and it may have invaded the interior of each prism from all its edges at once. In such cases all that is left of the original prismatic layer is a series of elongated kernels (already altered during the first stage in diagenesis) surrounded by lighter coloured microcrystalline calcite of the second stage. These kernels may be regular in appearance, but are sometimes truncated by a 'front' of second-stage microcrystalline material, where the latter has grown more rapidly in one direction than in others (Pl. 50, fig. 8).

Recrystallization of primary structures is less easy to recognize in fracture surfaces or in etched sections using the Stereoscan. It has been observed, however, that whereas certain calcite prisms have sharp, well-defined corrugations on the surface, parallel with the cleavages, other calcite crystals in the same eye may have much less regular corrugations, and only a rough granularity to the surface. As unaltered primary crystals have well-defined cleavages, it would seem likely that the crystals with roughly granular surfaces have undergone some measure of diagenesis.

Secondary growths below the primary prisms. In one specimen (Gr I 5508), both fracture surfaces and thin sections revealed inward extensions of the primary prisms.

EXPLANATION OF PLATE 49

Asaphus raniceps Dalman (Stereoscan photographs, all of fracture surfaces).

Fig. 1. Slightly oblique view of primary prisms (corrugated), with smooth secondary (diagenetic) prisms growing syntaxially upon them. × 180. Gr I 5508 (cf. text-fig. 2).

Fig. 2. Lower terminations of the same secondary prisms and subjacent area of recrystallized calcite. × 130. Gr I 5508 (cf. text-fig. 2).

Fig. 3. Several prisms underlying the cornea, visible as an upstanding wall near the top of the photograph. Two adjacent prisms are fractured showing a common cleavage direction running through both. × 325. Gr I 5506.

Fig. 4. Junction between primary and secondary prisms (cf. Pl. 49, fig. 1). × 485. Gr I 5508.

Fig. 5. Enlarged surface of corrugations on the outer surface of a prism (cf. Pl. 48, fig. 2). × 2400. Gr I 5504.

Fig. 6. Prisms near the lower margin of the visual surface. × 65. Gr I 5505.
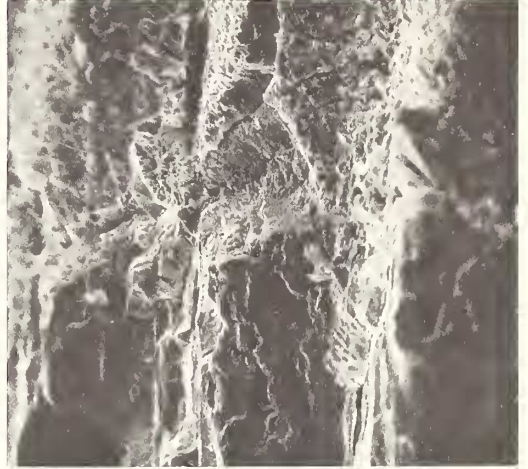
PLATE 49

CLARKSON, *Asaphus* eyes
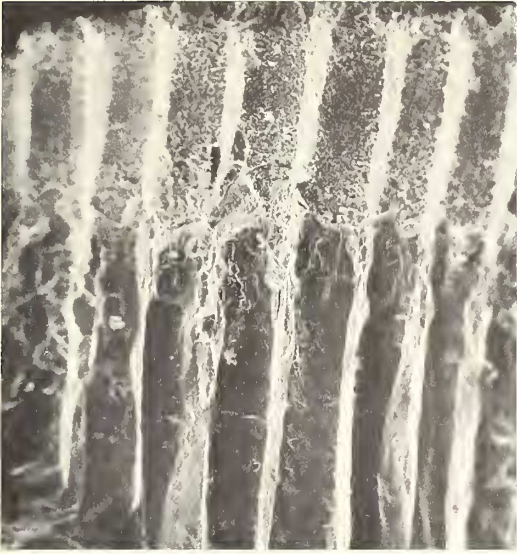
Stereoscan photographs showed these to be of extremely regular form, being syntaxial, pillar-like extensions of the outer prisms (Pl. 49, figs. 1, 2; text-fig. 2a, b). They are found only in certain parts of the eye, and in all the Stereoscan preparations extend to about the same level. Between and around these areas lie micrite and finely recrystallized sparite, in patches. These extensions, referred to as 'inner' or 'secondary prisms', have very smooth outer surfaces, and the transition from the corrugated outer zone is sharp, being marked usually by a line of somewhat irregular fractures (Pl. 49, fig. 4). One example showed the edges of a primary prism being met by the sides of an inner prism, but normally the edges of a primary prism are continuous with those of a secondary one.

Below the inner prisms (sub-prismatic region in text-fig. 2) are large, equant calcite crystals with patches of micrite and sparite. Some of these are syntaxial with the inner prisms. Several orientated crystals of dog-tooth spar cemented together by a calcitic jacket were noted in one area; these had near-perfect crystal faces.

Though there would be little doubt that all the structures in this sub-prismatic
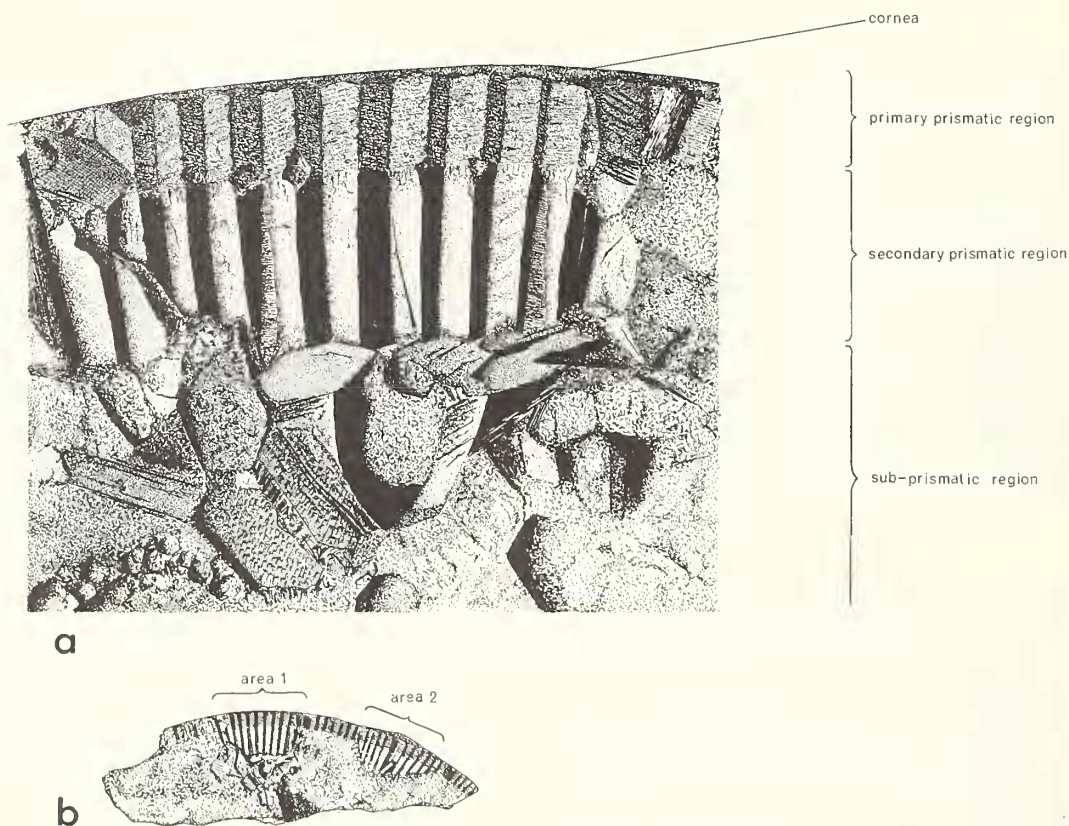
TEXT-FIG. 2. Drawings made from fracture surface of Gr I 5508 showing areas of primary and secondary (diagenetic) calcite. a. Enlargement of area 1 × 120. b. Fragment of eye showing the two areas of secondary prisms, one of which is enlarged in a. × 18.

region are secondary, the regular appearance of the inner prisms in the Stereoscan photographs might suggest that at least these could be of primary origin, though other Stereoscan evidence is equivocal. Thin sections, however, indicate that the inner prisms are very probably secondary. The series illustrated in text-fig. 3*a–c* are vertical sections made obliquely through the posterior region of the eye of Gr I 5508.

Text-fig. 3*a* (Pl. 50, fig. 3) shows a cellulose acetate peel stained with methylene blue (Dickson 1966). The primary layer has been differentially affected by first-stage diagenesis, though crystal boundaries are clear in places. There is a pronounced
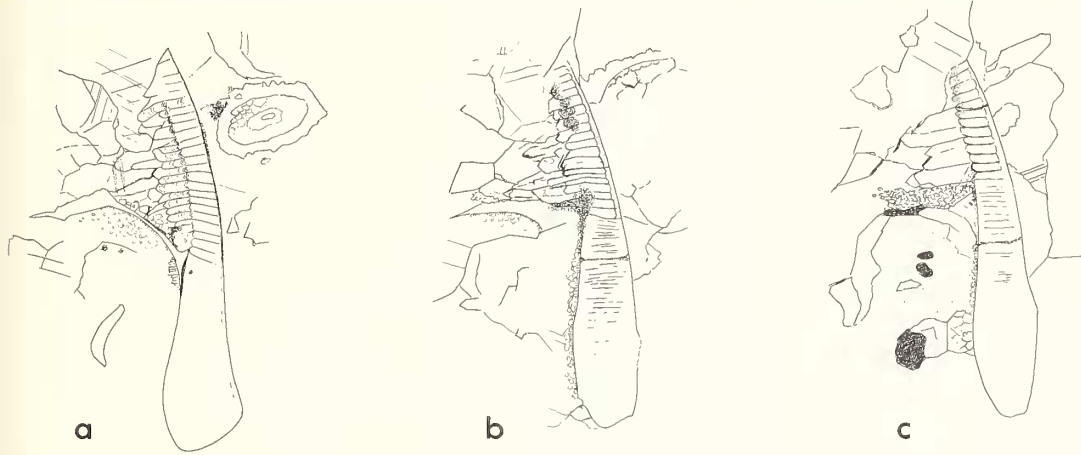
TEXT-FIG. 3. Effects of diagenesis shown in thin sections and cellulose peels of Gr I 5502. *a*. Oblique vertical section near posterior margin stained with methylene blue, showing primary and secondary prisms. *b*. Similar section, stained with alizarine red-S and acid fuchsine, with very irregular secondary prisms. *c*. Thin section through the same area, showing complete recrystallization of the secondary and partial alteration of the primary prisms. All × 20.

line of demarcation between the primary and the inner prisms. The latter, though regular in places, are elsewhere of differing lengths, and sometimes overgrow one another. They show clear evidence of secondary growth on the bases of the primary prisms in that a record is left of the past position of the euhedral crystal faces. The structure becomes very irregular at depth, but even here some crystals are still more or less syntaxial with the primary prisms. Similar, though much smaller, secondary growths were visible in other calcitic shells in the same section.

Cellulose peels stained with alizarine red-S and acid fuchsine (Pl. 50, fig. 2; text-fig. 3*b*), through the same general region but more posteriorly, showed much the same kind of structural elements but picked out slightly different details. The section illustrated was more strongly affected by second-stage diagenesis, and the boundary between primary and secondary structures was indistinct. In general, there was far less regularity, which emphasizes the secondary nature of the inner prisms. This section also showed a fringe of small secondary calcite crystals, elongated and with axes normal to the surface of the cuticle, growing on the inside of the eye-socle. These are clearly analogous to the inner prisms.

In an optical thin-section (Pl. 50, fig. 8; text-fig. 3*c*), there are very large elongated euhedral crystals, growing below the primary layer, each encompassing the bases

of several (altered) primary prisms. They are in optical continuity with the latter, though these are altered by first-stage diagenesis, but they are not in optical continuity with the light yellow material of the second diagenetic stage. Probably these large euhedral crystals resulted from the coalescence of several smaller crystals which originated in contact with the primary prisms.

It is clear from the foregoing observations that all the calcitic elements below the primary prismatic layer are of secondary origin. The great regularity of their structure in some parts of the eye (which is not always maintained in other regions) is merely a reflection of the regular arrangement of the large prisms above, which provided suitable foci for continued growth of calcite, provided that there was a void below. It may have been that there were partially calcitized elements below the primary prisms which could have controlled the direction of subsequent calcitization, but there is no direct evidence of this.

VISION IN *ASAPHUS RANICEPS*

Visual field. A provisional determination of the visual field has been made, using similar apparatus and techniques to those described formerly (Clarkson 1966a, b). Since the prisms are normal to the surface it was possible to use a graticule and protractor to measure the inclination of the upper and lower margins of the visual surface, every 10° of longitude from front to rear, in a manner comparable with the measurement of the axial bearings of individual phacopid lenses. Plotting these inclinations on a Lambert net gave an angular range of vision quite similar to that of many phacopids (text-fig. 1g), overlapping at front and rear to give some degree of binocular vision. The relatively narrow latitudinal extent of vision may be contrasted with that of many holochroal eyes, where latitudinal ranges of up to 120°


EXPLANATION OF PLATE 50

*Asaphus raniceps* Dalman (Photomicrographs of thin sections, except Figs. 2 and 3 which are acetate peels).

Fig. 1. Horizontal section through eye showing the cleavages running through the prisms and the rounded terminations of the latter. Plane polarized light. ×80. Gr I 5512.

Fig. 2. Oblique vertical section (acetate peel) stained with alizarine red-S and acid fuchsine, with very irregular secondary prisms. ×65. Gr I 5502 (cf. text-fig. 3b).

Fig. 3. Similar section (acetate peel) stained with methylene blue, showing primary and secondary prisms. The latter are rather irregular and exhibit growth lines. ×65. Gr I 5502 (cf. text-fig. 3a).

Fig. 4. Oblique vertical section showing primary prisms only. ×18. Gr I 5511.

Fig. 5. The same under crossed nicols. ×18. Gr I 5511.

Fig. 6. Part of vertical section through an eye somewhat altered by first-stage diagenesis, showing primary prismatic layer, with indistinct prisms, and the thin cornea (lower part of this section in fig. 9). ×40. Gr I 5503 (cf. text-fig. 4c).

Fig. 7. Part of a vertical section, showing advanced diagenesis, passing through the uppermost part of the visual surface (upper marginal zone of Lindström). ×80. Gr I 5503.

Fig. 8. Oblique vertical thin section showing complete recrystallization of the secondary prisms and partial alteration of the primary prisms. ×37. Gr I 5502 (cf. text-fig. 3c).

Fig. 9. Downward continuation of section in Pl. 50, fig. 6, showing inward extension of a sensory fossette and the upward passage of the vertically laminated outer cuticular layer of Dalingwater into the cornea at the base of the eye-socle. ×40. Gr I 5503 (cf. text-fig. 4c).

PLATE 50
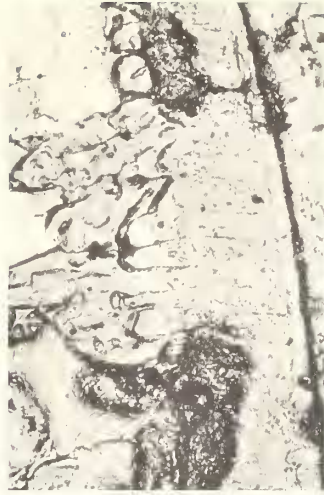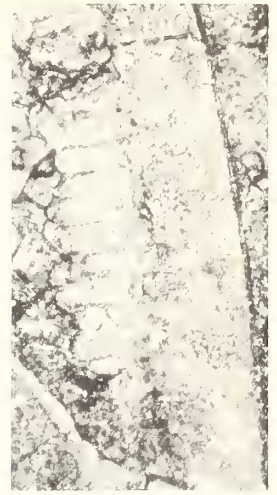
CLARKSON, *Asaphus* eyes

for each eye, with marked overlap above, are not uncommon. This plot represents the minimum possible range of vision, assuming that the peripheral prisms receive only light coming parallel with the c-axis. The eye may have actually been capable of receiving light from outside this zone and transmitting it to the photoreceptors; this would depend upon whether or not screening pigment was present, isolating the ommatidia as in modern compound eyes.

Optics of the calcite prisms. Calcite was used as a primary structural component in trilobite cuticle. It was also present in the eye, where it was of particular value, being rigid, easily secreted in the same way as the rest of the cuticle, and above all refractive and transparent. But calcite is an anisotropic mineral with the property of double refraction, and its use in an optical system raises problems. Some modern arthropods have an irregular mosaic of calcite crystals within the eye as mentioned earlier.

In the following discussion on calcite optics each prism is considered as an individual calcite crystal, though it is recognized that each was probably penetrated throughout by organic matter. How far this would have altered the refractive index, if at all, cannot be assessed but the birefringent properties of calcite would not have been eliminated by such interpenetration. The calcite cornea may also have had an organic association.

Each prism is a single hexagonal crystal with its optic axis (c-axis) normal to the surface of the eye. Any light rays entering the crystal normal to the visual surface (i.e. parallel with the optic axis) would be transmitted, unpolarized, straight through the crystal without any change of direction. A light ray entering obliquely, however, will be resolved into two linearly polarized rays vibrating perpendicular to each other. The ordinary ray has constant velocity whatever the direction of incidence, but the extraordinary ray increases in velocity as the angle of incidence increases from the normal. Oblique incident rays not only polarize, but produce double images at different depths. Herein lies the disadvantage of calcite; some interference with the visual process would be expected, unless there were some system within the eye for ensuring that only normal or near normal rays were actually let through to the photoreceptive organs below.

Let us consider the angular light receptivity of each crystal. Median sections of two crystals, of the dimensions actually found in different parts of the eye, are illustrated in text-fig. 1e, f. Text-fig. 1f is the typical form, occurring in all but the peripheral regions of the eye, whereas text-fig. 1e is a crystal from the generative zone hear the lower margin. If each prism is considered as an isolated unit, the most oblique incident ray which it could transmit would be refracted along the line XY which is the path and wave-normal of the ordinary ray.

Light entering at a higher angle of incidence would be refracted against the wall of the prism. The angle of incidence for such a refracted ray travelling along the line XY can be calculated using Snell's Law and the following refractive indices ($n_{water} = 1.33$, $n_{o-ray} = 1.66$). The highest angles of incidence are then 44° and 22° respectively for the two prisms. If $n_{e-ray} = 1.48$, then using the optical indicatrix for calcite, the path of the extraordinary ray incident at O may be constructed as in the diagram; as it travels faster it is less highly refracted. Thus each prism, considered by itself, has quite a high range of angular receptivity.

The prisms in the eye do not, however, exist in isolation, but are contiguous one with another. It is not known, of course, whether in life they were optically separated by organic layers along their walls. There is no evidence of such layers, and their former presence is rendered unlikely both by the close contiguity of the prisms and the fact that there are small domains of optically associated prisms where the cleavages pass through from one crystal to another. The lenses of modern insect and crustacean eyes, where contiguous like those of *Asaphus*, are sometimes optically isolated one from another by such highly refractive layers but not always, and indeed the superposition system of vision, as mentioned later, depends upon their close optical contiguity.

If, therefore, as we assume, the prisms of *Asaphus* were originally in optical contiguity, then the dioptric system as a whole would actually be receptive to a much higher range of light incidence, for the light could pass through neighbouring crystals. In such a case the divergence between the path of the extraordinary and the ordinary ray would increase, resulting in more extreme double refraction and hence double images at different depths.

Such double images, however, could have been virtually eliminated and not transmitted to the photoreceptors if the *Asaphus* eye were provided with a layer of absorbing pigment, just below the prismatic region, exactly as with the 'distal retinal pigment' of many known crustaceans (text-fig. 4*d*, *e*), which occurs in both apposition and superposition eyes. In the latter, there is a cylindrical sleeve of black or brown pigment surrounding the upper parts of each ommatidium below the lens, embracing the crystalline cone and the area below it, which absorbs unwanted light rays. A similar pigment sleeve in *Asaphus* located just below the prisms, would fulfil an identical function, and if the central bore were narrow, would effectively restrict most of the oblique rays, and screen them from the other ommatidia. If this were the case a mosaic-type image could then be formed by the eye, using only rays parallel with the axis or only slightly oblique and thus cutting out most of the adverse effects of double refraction. Such a system would allow a degree of mosaic vision not greatly inferior to that of modern arthropods. The extreme sphericity of the visual surface would give a more or less undistorted image of the mosaic kind, and it might also relate to a kind of superposition vision, as discussed in the next section.

Arrangement of deeper-lying structures. The visual surface of *Asaphus raniceps* has an almost constant horizontal curvature, the radius of which is slightly less than that in the vertical plane, though the latter is less regular, and decreases towards the top of the eye. Thus the visual surface approximates a segment of a prolate spheroid in which the vertical axis is slightly greater than the horizontal ones.

The eye has a slightly higher profile curvature anteriorly than posteriorly, and the visual field is expanded latitudinally towards the front (text-fig. 1*g*). Apart from this slight difference the curvature of the eye is otherwise regular, and follows the almost perfectly radial arrangement of the primary prisms. In horizontal and vertical sections of well-preserved specimens the edges of the prisms are clearly visible, and may be used as a basis for some reconstruction of the internal parts. If lines are drawn along the edges of adjacent prisms and extended inwards, they are found to meet at a common centre.
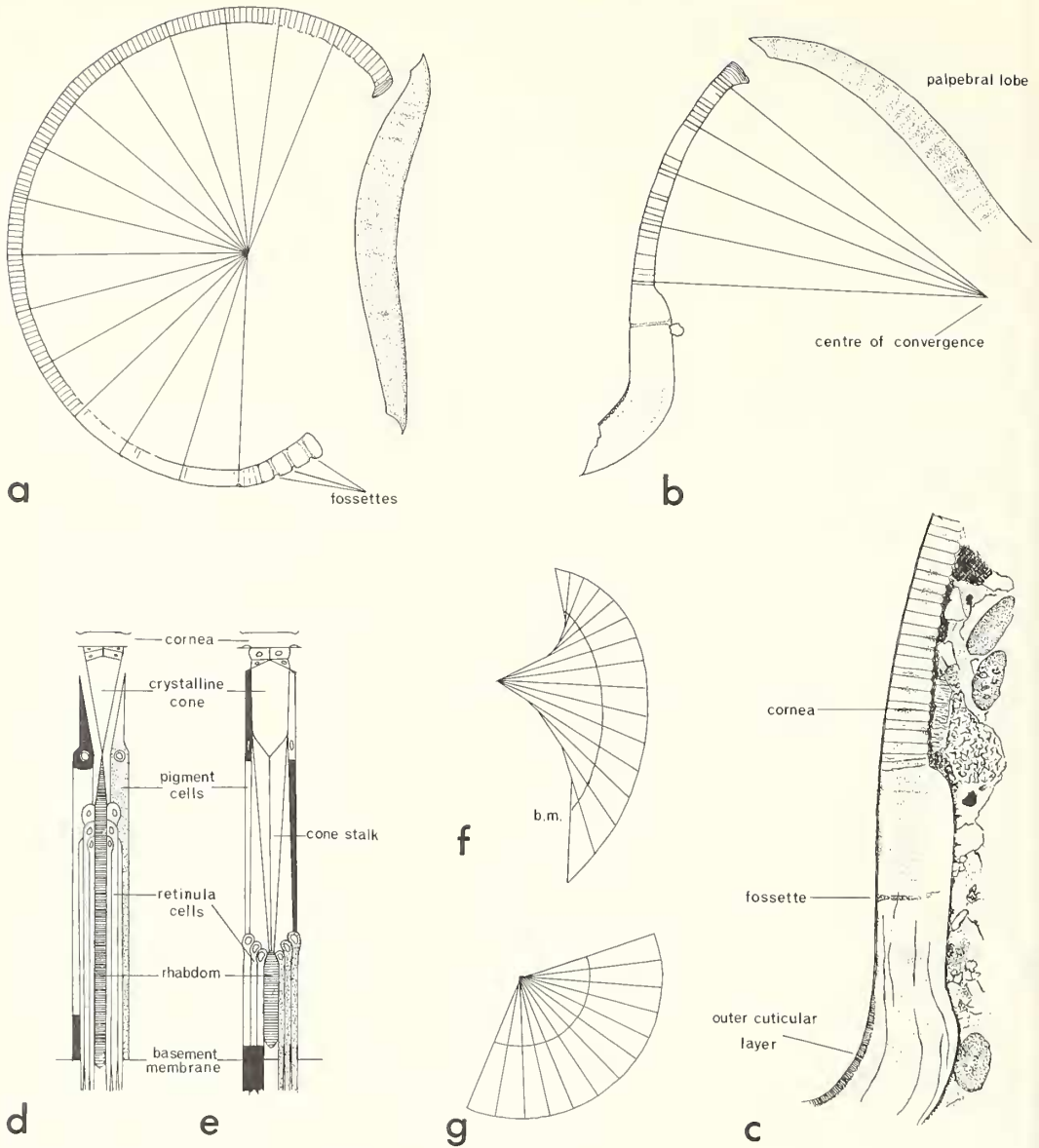
TEXT-FIG. 4. *a*. Horizontal section through *A. raniceps* eye, with radii of curvature passing through every tenth prism marked. From a thin section. ×12·5. Gr I 5512. *b*. Vertical section. ×12·5. Gr I 5503. *c*. Thin section through lower part of visual surface and eye-socle. The outer cuticular layer of Dalingwater passes upwards into the cornea at the base of the eye-socle. ×30. Gr I 5503. *d*. A single ommatidium of the apposition eye of a shore crab. *e*. Ommatidium of the superposition eye of a lobster.

In *d* and *e*, the left-hand side is shown as dark-adapted, the right as light-adapted. Both after Kampa (1965).

f, *g*. Diagrams illustrating surface convexity and centres of ommatidial convergence in the eyes of the insect *Apis mellifica* (apposition eye), and *Samia cecropia* (superposition eye). Both redrawn from Portillo (1936).

The radii of curvature in the two directions are illustrated in text-fig. 4*a*, *b*. It is very probable that those parts of the eye, now destroyed, lying below the primary prisms, were elongated ommatidia, following the radii of curvature more or less exactly, just as in the eyes of many insects and crustaceans, though how deep they were cannot be assessed. In modern arthropods the first optic ganglion of synaptic region occupies the central part of the underlying space and the same was probably true of the trilobites. Almost certainly the ommatidia must have terminated some distance short of the centre of curvature.

The regularity of surface curvature, ommatidial separation, and radial arrangement of the ommatidia, evident in *Asaphus raniceps*, is also characteristic of the structure of many superposition eyes in modern arthropods. In this respect the eye of *A. raniceps* is unlike both modern apposition eyes, and those of phacopid trilobites.

Anatomical differences between apposition and superposition eyes are very well known, and have been synthesized in various reviews (Waterman 1961; Goldsmith 1964; Wigglesworth 1965). Apposition eyes (text-fig. 4*d*) have the rhabdom in contact with the crystalline cone, whereas in superposition eyes (text-fig. 4*e*), the cone and rhabdom are separated by a long cone-stalk, believed to be a light conductor. The rhabdom here is very much shorter than in apposition eyes.

These anatomical differences have been greatly discussed since the time of Exner (1891), but their physiological significance is still controversial (Goldsmith 1964; Miller *et al.* 1968).

Superposition eyes, which are typical of nocturnal crepuscular or deep-water arthropods, have an elaborate system of adaptation to dark conditions. In light-adapted superposition eyes, when screening pigment surrounds each ommatidium, the visual system probably forms a mosaic image rather like an apposition eye. (Actually the 'mosaic theory' of image formation, first propounded by Müller in 1826, is now held to be too simple, and Burtt and Catton (1962, 1966*a*, *b*) have shown the important role of diffraction processes in arthropod vision, so as to modify greatly and extend the mosaic theory.)

In dark-adapted superposition eyes, the pigment migrates away from the cone-stalk region so that the isolation of the ommatidia is lost. In this way light coming through many lenses can pass freely to any rhabdom, and is not confined to any specific ommatidium. Sensitivity seems to be increased thereby, though resolution is lost.

It is interesting that the only modern arthropod eyes of spherical, geometrically perfect form with the radii meeting at the centre are of superposition type (Portillo 1936), though not all superposition eyes do, in fact, have such perfect form. Portillo believed that such a structure was highly desirable for superposition vision, both optically and physiologically.

The parallels between the regular structure of the eye of *Asaphus raniceps*, and typical modern superposition eyes are illustrated in text-fig. 4*a*, *b*, *f*, *g*; it is possible that the number of points in common may imply some degree of functional similarity.

Some recent work by Stuermer (1970) appears at first sight to militate against the above suggestions. Stuermer subjected the schizochroal eyes of some Devonian phacopid trilobite to X-ray examination and found within the eyes very long, closely

B

packed bundles of fibres extending from the lentiferous region right into the axial part of the body of the trilobite. He interpreted these as light guides (presumably equivalent to very long cone-stalks in modern arthropods), which conducted light from the lenses to the photoreceptors.

I have assumed that in *Asaphus raniceps*, as in virtually all recent arthropods, the photoreceptive organs were of ommatidial kind, arranged radially, following the radii of curvature more or less exactly and that optic ganglion was present centrally. Though Stuermer's material is tectonically distorted, it is clear that the structures he described do not follow this pattern; they are numerous and quite thick and because of their extreme length a radial pattern is not evident. As far as can be seen they terminate outside the optic region altogether so that if they were really light guides the optic ganglion would be displaced towards the central part of the body.

Thus the eye as interpreted by Stuermer bears very little resemblance to any other kind of arthropod eye. Even in certain mysids and euphausiids where the cone-stalks are of exceptional length (thus accommodating multiple diffraction images at different depths), the optic ganglion remains centrally located, and the external part of the eye becomes expanded outwards during ontogeny to accommodate the extra length. It is difficult to see what purpose could be served in the large-lensed phacopids by such an improbable distance between lens and photoreceptor, and it is likely that the fibre-bundles are not part of the optical system at all. They could be part of a circulatory system like the alimentary prosopon of many Cambrian trilobites (Öpik 1961) only located below the surface, or, as Dr. J. Bergström (pers. comm.) has suggested, filaments of the 'gill' or exite branch of the appendages. Various factors seem to support this suggestion, and in particular the random and oblique orientation of the fibre-bundles, and their indistinct preservation directly below the palpebral furrow, which would have acted as a ridge crushing against the filaments. Such filaments may have been preserved only where trapped in the void below the eye and the glabella, and that is why they extend only to the visual surface and not beyond, thus giving the impression of being part of the optical system.

Until further evidence is forthcoming, therefore, Stuermer's structures cannot be unequivocally accepted as being light guides. And though the internal organization of the schizochroal system may well have differed from that of holochroal eyes the external morphology of the latter approximates that of insects and crustaceans in so many ways that it seems more appropriate to infer some internal resemblance, at least in so far as having radially arranged photoreceptors and a centrally placed ganglion.

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